

Falsification of an entomological rule: Polymorphic genitalia in Geometrid moths

(Lepidoptera, Geometridae)

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In this paper the universal validity of a widely accepted convention in the taxonomy of insects, i.e. the strict correlation between diversity of genitalia and species diversity, is refuted on the basis of some examples from the lepidopterous family Geometridae.

Many species of the Geometrid moth genera *Scopula* Schrank, 1802, and *Glossotrophia* Prout, 1913, show infrapopular polymorphic patterns in the structure of the lateral processi (“cerata”) of the sternite 8. This phenomenon must refer to polymorphism and not to species diversity, since specimens of the various sternite types have been reared from the eggs of one single female.

Two series of specimens, in which one genitalic feature differs in a statistically significant way, cannot be interpreted as different species due to this discontinuous diversity only. Taxonomists should apply particular caution, when there are already known polymorphisms in the genitalia of related species, e.g. in the above mentioned genera. To date nearly 20 taxa on species or subspecies level are known to have true polymorphic structure of the sternite 8.

Each species with polymorphic genitalia has closely related species, which do not show such multiple patterns. Since polymorphic genitalia are a very unusual phenomenon in Lepidoptera and are unlikely developed a several times independently, the most parsimonious hypothesis is to assume silent genes in the phylogenesis of the genera *Scopula* and *Glossotrophia* to be responsible for the heterogeneity of the expression of this feature.

Key words: Polymorphism; silent genes; phylogeny; taxonomy; genitalia, Geometridae, *Scopula*, *Glossotrophia*.

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Introduction

More than 50 years ago Sterneck (1940, 1941) revised the palearctic taxa of the Geometridae subfamily Sterrhinae including about 400 species. To date the results of this fundamental work are generally accepted and applied, almost without discussion or modification. In his introduction Sterneck (1940: 7) presents the following two guiding principles to base upon his scientific research:

- 1) “Species diversity has to be postulated, where ‘diversity’ in the genitalia is found”.
- 2) “Forms with the same genitalia belong to the same species”.

“Diversity” has to be defined *sensu* Sterneck as two series of specimens with at least one different genitalic feature which is morphometrically measurable and does not show continuous transitions due to variability (compare Sterneck 1940: 7).

Today, the universal validity of Sterneck’s second principle is often drawn into doubt in lepidopterology. Examples of species have been reported, which can be clearly distinguished from their sister species by features of wing pattern, external morphology, pheromones and/or ecological niche, but do not have valuable differences in the genitalia (e.g. Weigt 1988: 47, 1991: 22).

The first principle of Sterneck however has never been explicitly and seriously drawn into doubt. Also Träff (1965: 134) is convinced, that “the structure of the “mappa” and particularly of the “cerata” in the sternite 8 of the genus *Scopula* (Geometridae, Sterrhinae) is constant and characteristic for the separation of species”. Most taxonomists in entomology consider Sterneck’s first principle to be valid as tacit understanding (e.g. Petersen 1909: 203ff., Pierce 1914: XV, Wehrli 1954: VIII f., Berio 1985: 43f., Scoble 1994: 101), even if many are aware of certain limitations: For example Svensson (1967) and Holloway (1997) figure polymorphic genitalia for two different species of the genus *Scopula*, but they refer this phenomenon to continuous “variation” postulating intermediate forms.

The present study has the aim to refute on the basis of some concrete examples the universal validity of Sterneck’s hypothesis of strict correlation between diversity of genitalia and species diversity. These examples have been found exactly in the subfamily Sterrhinae, which had been revised by Sterneck.

Material, methods and definitions

Material. In the last ten years the author studied the morphology of some thousands of specimens of the genera *Scopula* Schrank, 1802, and *Glossotrophia* Prout, 1913, stored in the Zoologische Staatssammlung München (ZSM). Genitalic structures of about 1.300 specimens have been examined after dissection. Some type specimens and further material from other museums have been additionally controlled.

Methods. Taxonomical work on the collection material has been done applying the ‘usual’ methods of morphological analysis of external and internal features (e.g. genitalia). Measurements have been done using a stereo microscope with an ocular micrometer. Several females of *Glossotrophia alba brunellii* Hausmann, 1993, which have been caught by the author in the years 1992 and 1993 in Southern Italy were taken into captivity to deposit their eggs. This mediterranean species can be reared successfully on *Silene vulgaris* even in Central Europe under laboratory conditions. The emerging moths of the F1 generation were subsequently reared under controlled conditions (father and mother identified and labelled). The emerging descendants of the F2 generation were labelled indicating the identity of the parent specimens. 17 rearings have been made, of which only the more important will be discussed in this article.

Definitions. According to the generally accepted terminology (Klots 1970) the term “genitalia” or “genitalic structure” is understood functionally in this study and includes in the genera *Scopula* and *Glossotrophia* even the sternite 8. Since the length of the valvae is fairly reduced and the sternite 8 is particularly modified and sclerotized, it is fairly probable, that the latter bears some mechanical function in the copula. Functional morphology of genitalia however still waits for detailed investigations in the genera *Scopula* and *Glossotrophia*. In both genera the genitalia often do not bear any differential features at all, except for the sternite 8, which shows stronger diverging differentiations. For this reason to date taxonomic studies dealing these genera traditionally base mainly on differential diagnostic features of the sternite 8.

The terminology of structure details follows in this article that having been established by Prout (1913: 51) and Sterneck (1940, 1941): The paired, pointed, sclerotized processes, extending caudad from caudal part the sternite 8 are called “cerata” (singular: ceras). “Mappa” is the flat, weakly sclerotized plate between these cerata in the caudal part of the sternite 8 (Klots 1970). The terminology of the various sternite types (polymorphic individual forms) is no more based on latin form names (Hausmann 1993a), but on easily understandable codes of letters as follows:

SS = sternite symmetrical; both cerata very short (Figs 1, 4, 7)
 SL = sternite symmetrical; both cerata long, i.e. exceeding mappa (Figs 3, 6, 9, 12, 14, 16)
 ASM = sternite asymmetrical; one ceras short, the other one of medium size (Figs 15, 17)
 ASL = sternite asymmetrical; one ceras short, the other one long (Figs 2, 5, 8, 18)
 AML = sternite asymmetrical; left ceras of medium size, right ceras long (Figs 11, 13)

Results

In the run of routine examinations of the sternite 8 in some species of the genera *Scopula* and *Glossotrophia* strange variants have been found, which were strongly aberrative from the normal type (see figs 1-18).

Some Lepidoptera species are known to show considerable variations in male genitalia, as it has been discussed for a Coleophorid species in Itämies & Tabell (1997) and for the Crambidae in Amsel (1951). However the above mentioned variants of Geometrid moths do not represent extreme forms of a continuous intrapopular distribution of varying features. Intermediate forms do not exist in these populations. Morphometrical measurements lead always to two or three different series, in this article called "sternite types", with no overlap between groups (see figs 19a-d, tab. 2).

In a first working hypothesis the author suggested, that this result could indicate the existence of complexes of sister species. This hypothesis became more and more improbable, since in none of these

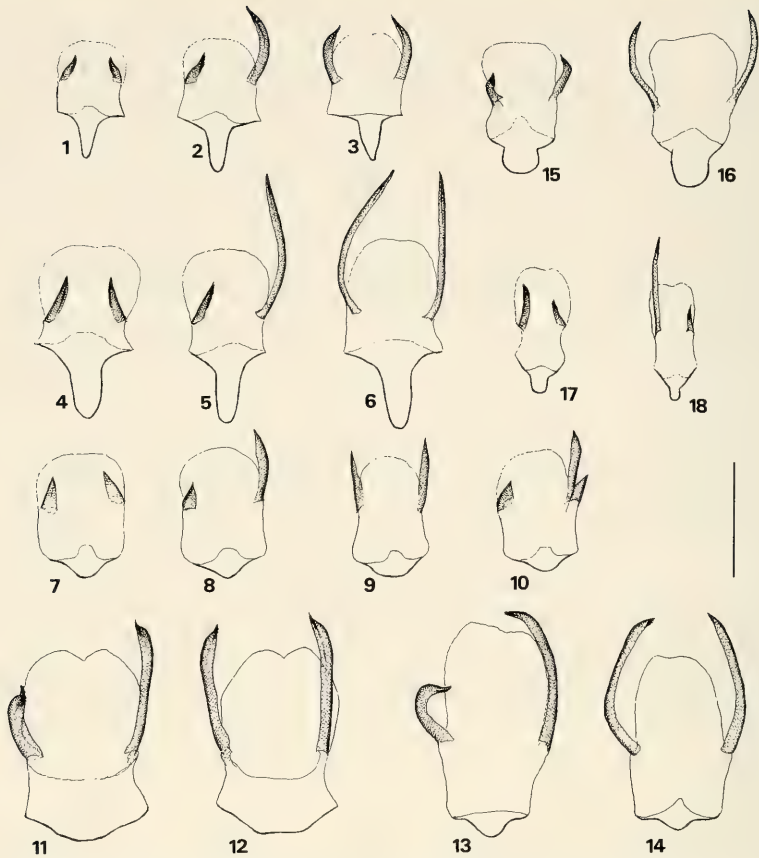
Tab. 1. Species with true polymorphic feature patterns in the cerata of the 8. sternite of the male: Percentages of the various sternite types in light catches in the field. n = number of dissected males.

sternite type	SS	ASM	AML	ASL	SL	n
<i>Glossotrophia confinaria</i> (Herrich-Schäffer, 1847) (N Italy)	–	–	–	70 %	30 %	37
<i>Glossotrophia confinaria</i> (Herrich-Schäffer, 1847) (Makedonia)	5 %	–	–	81 %	14 %	21
<i>Glossotrophia diffinaria</i> Prout, 1913 (Turkey)	21 % ¹	–	–	37 % ¹	42 % ¹	19
<i>Glossotrophia alba alba</i> Hausmann, 1993 (C Italy)	11 %	–	–	87 %	2 %	45
<i>Glossotrophia alba brunellii</i> Hausmann, 1993 (S Italy)	8 %	–	–	92 %	– ²	25
<i>Glossotrophia mentzeri</i> Hausmann, 1993 (Crete)	5 %	–	–	85 %	10 %	39
<i>Scopula (Ustocidalia) ternata</i> (Schrank, 1802) (N Europe)	5 %	–	–	90 %	5 %	21
<i>Scopula (Scopula) transcaspica</i> Prout, 1939 (Turkey)	–	–	5 %	–	95 %	20
<i>Scopula (Scopula) transcaspica</i> Prout, 1939 (Turkmenistan)	–	–	67 %	–	33 %	12
<i>Scopula (Ustocidalia) subpunctaria</i> (Herrich-Schäffer, 1847) (SE Europe)	–	–	67 %	–	33 %	27
<i>Scopula (Ustocidalia) adelpharia adelpharia</i> (Püngeler, 1894) (C Israel)	–	26 %	–	–	74 %	23
<i>Scopula (Ustocidalia) adelpharia pharaonis</i> Sterneck, 1933 (S Israel)	–	89 %	–	–	11 %	28
<i>Scopula (Ustocidalia) adelpharia pharaonis</i> Sterneck, 1933 (Sudan)	–	47 %	–	–	53 %	15
<i>Scopula (Ustocidalia) minorata ochroleucaria</i> (Herrich-Schäffer, 1847) (Israel)	–	4 % ³	–	96 % ³	–	76

¹ geographical gradient: in E Turkey SL type dominant, in W Turkey ASL type and in N Turkey SS type more abundant. In Turkey often sympatrical occurrence of all the three types.

² present in rearing from the egg: 1/68 = 2 %.

³ left ceras longer than the right one here.



Figs 1-18. Sternite 8 (male) with polymorphic variants in some species of the genera *Scopula* and *Glossotrophia*. Scale bar = 1 mm. Ventral view. 1. *Glossotrophia alba brunellii* Hausmann, 1993; S. Italy, Maratea, reared from egg "6/93"; SS type. 2. *G. alba brunellii* Hausmann, 1993; S. Italy, Maratea, reared from egg "6/93"; ASL type. 3. *G. alba brunellii* Hausmann, 1993; S. Italy, Maratea, reared from egg "6/93"; SL type. 4. *G. diffinaria* Prout, 1913; C. Turkey, Gürün; SS type. 5. *G. diffinaria* Prout, 1913; C. Turkey, Gürün; ASL type. 6. *G. diffinaria* Prout, 1913; C. Turkey, Gürün; SL type. 7. *Scopula ternata* (Schrank, 1802); N. Norway, Mo i Rana; SS type. 8. *S. ternata* (Schrank, 1802); N. Norway, Mo i Rana; ASL type. 9. *S. ternata* (Schrank, 1802); N. Norway, Mo i Rana; SL type. 10. *S. ternata* (Schrank, 1802); N. Norway, Mo i Rana; aberrative with three cerata. 11. *S. transcaspica* Prout, 1939; Turkmenia, Kopet Dag; AML type. 12. *S. transcaspica* Prout, 1939; Turkmenia, Kopet Dag; SL type. 13. *S. subpunctaria* (Herrich-Schäffer, 1847); Serbia, Fruska Gora; AML type. 14. *S. subpunctaria* (Herrich-Schäffer, 1847); Serbia, Fruska Gora; SL type. 15. *S. adelpharia adelpharia* (Püngeler, 1894); C. Israel, En Gedi; ASM type (typical for "ssp. *pharaonis* Sterneck, 1933"). 16. *S. adelpharia adelpharia* (Püngeler, 1894); C. Israel, En Gedi; SL type. 17. *S. minorata ochroleucaria* (Herrich-Schäffer, 1847); C. Israel, Enot Zuqim; ASM type. 18. *S. minorata ochroleucaria* (Herrich-Schäffer, 1847); C. Israel, Enot Zuqim; ASL type.

cases any further differential feature (wing colour, external morphologic features, features in the rest of the genitalia) could be found, which were correlated with one of these genitalic variants.

Polymorphisms in the structure of sternite 8 seem to be a widely distributed phenomenon in the genera *Scopula* and *Glossotrophia*: Tab. 1 shows 14 examples with the respective field percentages of the different sternite types. Furthermore, multiple feature patterns concerning sternite 8 could be found for the following (sub)species: *Glossotrophia confinaria aetnaea* Prout, 1935, *Glossotrophia confinaria scoblei* Hausmann, 1993, *Glossotrophia asiatica* Brandt, 1938, *Glossotrophia* spec. nov. (N Iran), *Scopula ansulata* (Lederer, 1871) and *Scopula lactaria* (Walker, 1861). Of these taxa only small numbers of specimens (males) were available for dissection.

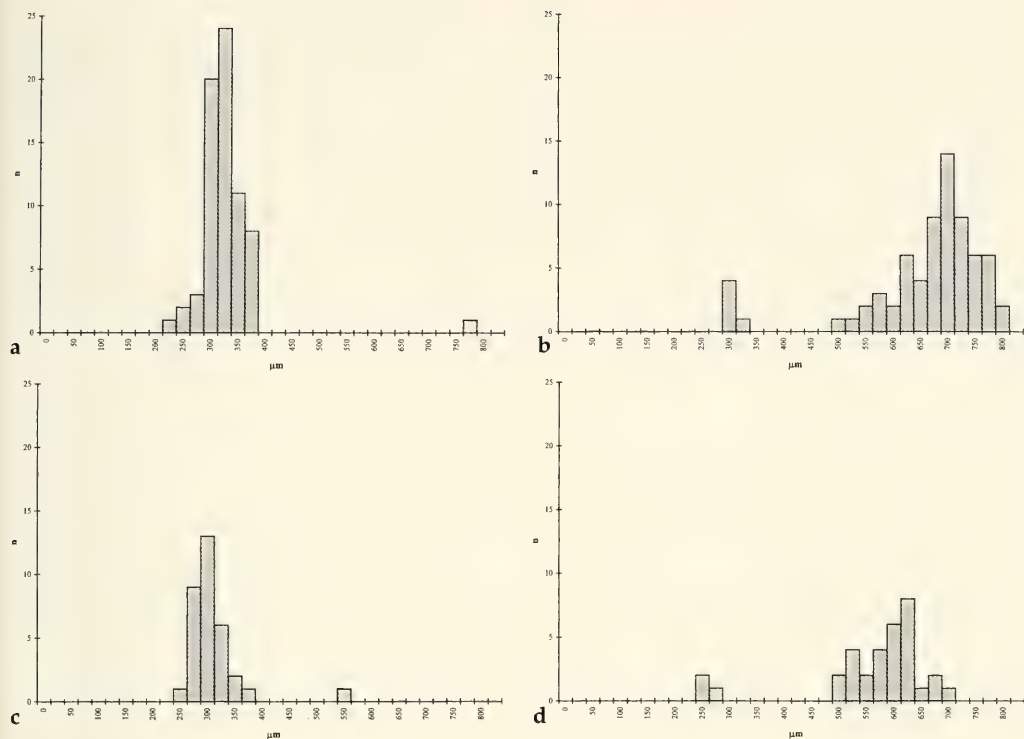


Fig. 19. Frequency distributions of length of cerata (sternite 8) in *Glossotrophia alba* from Central and Southern Italy; n = number of dissected males, μm = length of ceras in μm . **a.** Length of the left ceras in specimens from light catches (n=70). **b.** Length of the right ceras in specimens from light catches (n=70). **c.** Length of the left ceras in specimens from the rearing “6/93” (n=33). **d.** Length of the right ceras in specimens from the rearing “6/93”(n=33).

Tab. 2. Length of cerata (in μm) of the various sternite types of *Glossotrophia alba brunellii* from Southern Italy: Comparison light catches – specimens from rearing; m = mean, SD = standard deviation, n = number of dissected males.

object	sternite type	left ceras		right ceras		n
		m	SD	m	SD	
Light catches (1. gen.)	ASL	350	20	700	40	13
Light catches (2. gen.)	ASL	310	30	640	80	9
Light catches (2. gen.)	SS	380	0	350	0	2
F1 (rearing 2/93)	ASL	310	10	660	10	3
F1 (rearing 2/93)	SS	310	20	310	20	2
F1 (rearing 6/93)	ASL	310	30	590	50	29
F1 (rearing 6/93)	SS	270	10	260	10	3
F1 (rearing 6/93)	SL	550	–	600	–	1
F2 (rearing 9/93) (father ASL type from 6/96)	ASL	310	20	660	30	12
F2 (rearing 11/93) (father SS type from 6/96)	ASL	300	20	690	30	5
F2 (rearing 12/93) (father ASL type from 6/96)	ASL	310	10	660	40	5
Reared specimens (total)	ASL	310	20	630	60	54
Reared specimens (total)	SS	290	30	280	30	5
Light catches (total)	ASL	330	30	680	70	22
Light catches (total)	SS	380	0	350	0	2

The dry insect material stored at the ZSM gave first suggestions that such different types of the sternite 8 have been obtained from the rearing of the eggs of one single female (Hausmann 1993a: 286). For this reason the South Italian *Glossotrophia alba brunellii* has been caught and reared until the F2 generation. These experiments clearly revealed that such polymorphic feature patterns occur not only within a population but even in the rearing from the eggs of one single female (e.g. rearing "6/93", tab. 2). One male with a 'special' type of sternite 8 (SS type) has been taken for a subsequent rearing to F2, from which normal males emerged (see "11/93", tab. 2).

From the rearing "6/93" 33 males emerged as descendants of one single female. The distribution of the different sternite types shows a nearly identical feature pattern as it does in the comparison with the frequencies in light catches in the field (Figs 19a-d). Cerata are slightly longer in the field, which is due to the fact, that in this sample also moths from the first (spring) generation are included, which are somewhat larger. The emerging F1 generation in the rearing "6/93" did belong to the second (summer) generation.

Discussion

The results should implicate accurate discussions, because they throw light on interesting aspects of population genetics, phylogenetics and taxonomy. On the other hand they also raise some questions to be resolved in future.

As far as the **population genetics** is concerned, we can fix the following observations: Many species of the genera *Scopula* und *Glossotrophia* show infrapopular polymorphic feature patterns in the cerata of the male sternite 8. These are not due to individual random mutations, but are fixed genetically for the respective population in a characteristic distribution of frequency. It is proven by repeated rearing, that the different structural types do not refer to different sympatrical sister species, but to the same species.

Further investigations should clear up the way that the respective features are fixed genetically. The results of the rearing "6/93" (compare the chapter results) show too low frequencies of the 'unnatural' sternite variants, to think on one single mutated gene, which is expressed according to Mendel's rules. Even the corresponding percentages in the feature distribution between this rearing and the light catches in the field is remarkable in this context (compare figs 19 a-d).

The examined species show (in different typical patterns) the variation of the length of both the left or the right ceras. This variation occurs in all the presented species in this study without correlation with any other feature. In *Scopula lactaria*, *Scopula adelpharia adelpharia* and *Scopula adelpharia pharaonis* the reduction of the length of the cerata occurs obligatorily correlated in both cerata arms (Figs 15, 16), i.e. the reduction of one single arm has not been found. For the moment it must remain unclear, if this phenomenon is due to a genetical predisposition with bilateral symmetric influence or if there exist complexes of sister species in these cases.

One (rare) mutation in *Scopula ternata* with three cerata (Fig. 10) shows, that nature, apart the genetically fixed polymorphic variability, is always experimenting by individual random mutations too.

Interesting aspects result even for **phylogeny**: Despite extensive preparations of genitalia no structural variants could be found for the species *Glossotrophia rufomixtata* (de Graslin, 1863) and *Glossotrophia chalcographata* Brandt, 1938 (n = about 50 slides without polymorphic variation; Hausmann 1993b), which are both rather closely related to the polymorphic species *Glossotrophia confinaria*, *Glossotrophia diffinaria*, *Glossotrophia alba* and *Glossotrophia mentzeri*. The same must be stated for 12 furthermore examined species of *Glossotrophia* (n = about 300 slides without polymorphic variation; Hausmann 1993b). On the other hand, such polymorphisms occur in the same feature with exactly corresponding patterns in the genus *Scopula*: The similarity between the feature patterns of *Glossotrophia alba* and *Scopula ternata* is stupefying (compare figs 1-3, 7-9, and tab. 1). Many external and internal structural features clearly show however, that *Glossotrophia alba* and *Scopula ternata* are not even linked by congeneric relationship.

The predisposition to polymorphic variability can be found in both subgenera of the enormously species rich genus *Scopula* (*Scopula-Ustocidalia*). For all polymorphic *Scopula* species however there are closely related species without this predisposition. An example is the European *Scopula submutata* (Treitschke, 1828): this species is not polymorphic in the cerata of its sternite 8 even being very closely related to *Scopula transcaspica* (compare tab. 1).

As a conclusion we have to state a **mosaic pattern** of the feature “polymorphic cerata of the sternite 8” in both genera *Scopula* and *Glossotrophia*. Such phylogenetically heterogeneous patterns of parallelisms can be due to underlying synapomorphies: On the base of many examples Saether (1979) refutes too restricted ‘dogmatic’ criteria for synapomorphies, as e.g. postulated by Schlee (1971: 23), and defines underlying synapomorphies as “parallelism as a result of common inherited genetic factors including parallel mutations” (Saether 1979: 305). Since polymorphisms in genitalia are hitherto unknown in Lepidoptera, they have to be regarded as a fairly rare phenomenon. For this reason it is rather improbable, that during the phylogenesis of the genera *Scopula* and *Glossotrophia* the genetic predisposition for such a rare polymorphic feature pattern has been developed by parallel mutations sensu Saether so many times independently. The most parsimonious hypothesis is the assumption of “**silent genes**”, as they are postulated within the class of Insects for the Archaeognatha by Sturm (1994). Such silent, discontinuously active genes can be deactivated and reactivated from the “Kryptotype” (Osche 1965, Sudhaus & Rehfeld 1992) under conditions, which are little known to date. They probably are the reason for heterogeneous patterns of parallelisms not only in our example of the male sternite 8 in the genera *Scopula* and *Glossotrophia*, but for some further cases of apparent mosaic evolution, which are in discussion in the taxonomy of insects.

In the future the species of both Geometrid moth genera merit becoming objects of genetical investigations, e.g. for analysing the conditions for the reactivation of silent genes. They can easily be reared and the fast reproduction (trivoltine phenology e.g. in *Glossotrophia alba*) would suit such research projects.

In the **taxonomy** of insects the results of the present study are of high importance: The universal validity of the hypothesis “different genitalia refer to different species” (e.g. Sterneck 1940: 7, Träff 1965: 134; compare introduction) is clearly refuted by the present studies. In the differential analysis of two series of specimens the following steps reveal essential:

- analysis of the morphological variability (individual variation) on the basis of extensive material
- if possible, exclusion of the possibility of structure polymorphisms, by showing correlation to other features. This step is most important when there are already known polymorphisms in related species.

All taxa whose differential analysis to a sympatrical sister species was based on one single feature in genitalia should be checked for the possibility of polymorphism (e.g. by rearing)! Just one interesting example herefore: Träff (1965) described the Geometrid moth *Scopula aequicerata* as a new species for science. In more detailed studies it revealed to be only one of the different sternite types (SL type) of *Scopula ternata* and therefore synonym to the latter (fig. 9; tab. 1; Svensson 1967).

As far as the extremely species rich genus *Scopula* is concerned (actually known about 800 valid taxa on species or subspecies level) the presented results emphasize the necessity of a comprehensive revision. Many taxa, which have been described on the base of one single differential feature in the eighth sternite, will probably have to be synonymized. The genus *Glossotrophia* has already been revised by the author (Hausmann 1993a, 1993b, 1994).

Zusammenfassung

Falsifizierung einer entomologischen Grundregel: Genitalpolymorphismen bei Geometriden (Lepidoptera, Geometridae)

In der Taxonomie der Insekten wird oft eine strenge Korrelation von signifikanten Unterschieden im Genitalapparat und Artverschiedenheit als grundlegende Übereinkunft stillschweigend vorausgesetzt. Anhand einiger Beispiele aus der Lepidopterenfamilie Geometridae wird deren Allgemeingültigkeit widerlegt.

Viele Arten der Geometridengattungen *Scopula* Schrank, 1802, und *Glossotrophia* Prout, 1913, weisen in der Struktur der lateralen Anhänge des 8. Sternits (“cerata”) infrapopuläre polymorphe Merkmalsmuster auf. Da die jeweiligen strukturell unterschiedlichen Formen mehrmals aus Eizuchten ein und desselben Weibchens erzielt wurden, kann es sich bei diesem Phänomen nicht um Artverschiedenheit handeln.

Zwei Individuenserien, die sich in einem Genitalmerkmal statistisch signifikant unterscheiden, dürfen daher auf der alleinigen Basis dieses Unterschieds nicht als artverschieden interpretiert werden. Besondere Vorsicht empfiehlt sich dann, wenn bei nahe verwandten Taxa bereits Genitalpolymorphismen bekannt sind, wie z.B. bei bisher knapp 20 Arten und Unterarten der Gattungen *Scopula* und *Glossotrophia*.

Man findet Arten ohne multiple Merkmalsmuster neben nahen Verwandten mit polymorphen Genitalien, wobei sich letztere mosaikartig über die jeweilige Gattung verteilen. Angesichts der Seltenheit von Polymorphismen in Lepidopteren genitalien, erscheint dessen mehrmalige, voneinander unabhängige Entstehung im Lauf der Entwicklungsgeschichte unwahrscheinlich. Die sparsamste Erklärung ist als Arbeitshypothese daher die Annahme von 'schlafenden Genen' als Ursache der Heterogenität der zur Diskussion stehenden Merkmalsausbildung in der Phylogenie der Gattungen *Scopula* und *Glossotrophia*.

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